Land plant spores and the Ordovician–Silurian boundary

J. Gray

Department of Biology, University of Oregon, Eugene, Oregon, U.S.A. 97405

Synopsis

The size of early tetrad spores can be used to differentiate in a general way between late Ordovician and early Silurian rocks, although not to a fine degree of accuracy. No single trilete spores are found in Ordovician or earliest Llandovery rocks. Spores measurements are presented from the Ashgill of Bohemia, Canada and U.S.A. and the early Llandovery of U.S.A., Sweden, South Africa and Brazil.

Introduction

Early land plants can be traced through spores, having morphological analogues with spores produced by some living hepatics, back to the mid-Ordovician, about Llanvirn–Llandeilo time (Gray *et al.* 1982; Gray 1985), when recognizable remains, in terms of modern analogues, disappear. Abundant spores occur in a number of Late Ordovician (Ashgill) and in many early Silurian (Llandovery) rocks immediately above and below the Ordovician–Silurian boundary, and in some successions straddling the boundary as defined by marine invertebrates and phytoplankton. Spores occur in continental strata for this interval; they are principally abundant, doubtless related to intense weathering and often extensive metamorphism of continental rocks of this age (Gray & Boucot 1975), in shallow-water, nearshore marine rocks where other biostratigraphically useful microfossils and invertebrates are absent or inadequate for correlation. Land plant spores may ultimately prove to be the most useful fossils for helping to fix the approximate position of the Ordovician–Silurian boundary in that environment.

Gray (1985) assigned Late Ordovician-Early Silurian spores to Microfossil Assemblage Zone 1. MA Zone I is a homogeneous assemblage of spores of a single morphological type: compact tetrads arranged in a tetrahedral configuration with a mean size generally less than 35 microns, and usually smooth-walled. No single, trilete spores are found in Ordovician or earliest Llandovery rocks, although they appear, locally, in small numbers about midway through MA Zone I. Tetrads can be assigned for the most part to Tetrahedraletes cf. T. medinesis, although this does not necessarily mean that they all represent a single taxon, since spore 'morphological species' have different taxonomic values, representing anything from families and family groups to species or subspecies. Spore tetrads are found in Late Silurian assemblages but they do not dominate in the post-Early Silurian, where they are replaced by single trilete spores, smoothwalled and with varied types of wall ornamentation, which find their closest morphological analogue in spores of lower vascular plants. Locally, in Ordovician-Silurian rocks from the central and southern Appalachians and the midcontinent of North America, tetrads with a reticulate surface ornamention also occur in Microfossil Assemblage Zone I, beginning in the Ashgill and continuing through the early and middle Llandovery and early part of the late Llandovery. In North America, tetrads with other ornament types appear about midway through the Llandovery (Gray et al. 1986: fig. 5). Tetrads with reticulate surface ornamentation have also been found in samples from Gotland, Sweden, in earliest Silurian and Ordovician-Silurian boundary rocks but have not otherwise been convincingly identified elsewhere below the Silurian, although Vavrdová (1984) claims the presence of varied ornamentations among spore tetrads from the Kosov Formation of Bohemia. I did not see these on spore tetrads extracted in my laboratory from one rock sample kindly sent to me by M. Vavrdová.

Attention has focussed on the Ordovician-Silurian boundary, and the Ashgill, a time of glaciation and widespread marine regression, as one of a small number of intervals of mass extinction among marine invertebrates and phytoplankton. Spore tetrad assemblages show no

clearly defined changes across the Ordovician–Silurian boundary to indicate that land plants were in any way affected by the circumstances responsible for severe extinction in latest Ordovician shallow seas. There is no basic change in spore assemblages at the systemic boundary, no 'turnover' related to first or last appearances of spore types, or change in relative frequency of spore types on either side of the boundary.

The principal change that can be demonstrated for spore tetrads in Microfossil Assemblage Zone I is an increase in size from tetrads with average diameters under 30 microns in the Ordovician to tetrads with average diameters close to 50 microns near the end of Microfossil Assemblage Zone I in the mid-late Early Silurian (Gray *et al.* 1986). The consistent change in tetrad size is useful for determining the stratigraphical position within Microfossil Assemblage Zone I; change in tetrad size is less useful for discriminating the precise age of rocks to either side of the Ordovician–Silurian boundary, although tetrad size is useful for approximating the position of the boundary and for discriminating rocks close to the boundary from units of younger Llandovery age.

Spores are now known (Appendix, p. 356) from rocks deposited near the boundary from the midcontinent and Appalachians of North America; Manitoulin Island, Ontario, Canada; Brazil; Czechoslovakia; Gotland, Sweden; Libya; South Africa; and Arabia. At few of these localities is there independent information based on fossiliferous facies, shelly or graptolitic, bearing on the precise age relations of the rocks. However, marine palynomorphs (organic-walled phytoplankton: including prasinophyte phycomata and 'acritarchs') show an 'abrupt turnover' at the Ordovician–Silurian boundary related to change in phytoplankton assemblages coincident with extinction of many Ordovician species, in some southern Appalachian sections that are also spore-bearing. These have been used to position the systemic boundary in the absence of invertebrate fossils (Colbath 1983, 1985). In the absence of independent palaeontological evidence, the approximate stratigraphical position of measured spores assemblages relative to the Ordovician–Silurian boundary can be fixed, at least in North American sections, by the unconformity and lithological discontinuity at the systemic boundary itself (see Bergström & Boucot, this volume, p. 273).

Elmina Sandstone, West Africa

Spore tetrads have also been recovered from the Elmina Sandstone (lower Sekondi Series) from the vicinity of Sekondi-Takoradi, on the southwest coast of Ghana, West Africa. The Elmina was believed to straddle the Ordovician-Silurian boundary by Bär & Reigel (1980), who based their age assignment on marine phytoplankton ('acritarchs'), and in particular Dactylofusa, a taxon also found in strata assigned to the Itaim Formation, Maranhão (= Parnaiba) Basin, Brazil by Brito (1967: 480). Brito correlated his Palynological Zone T, from the Itaim, characterized by Dactylofusa maranhensis, with the Trombetas Formation of the Amazon Basin, regarded as 'probably Lower Silurian in its upper part and Upper Ordovician in its lower part' from the occurrence of *Climacograptus*, a taxon then mistakenly believed to occur only in the Lower Silurian. However, the marine, fossiliferous part of the Trombetas Formation can now be regarded as post-Lower Silurian (post-Llandovery) and probably Ludlow to possibly Gedinnian in age (Gray, unpublished spore data; P. Janvier, unpublished vertebrate data; F. Paris, unpublished chitinozoan data; L. Quadros, unpublished acritarch data 1985). Thus, Brito's assignment of Palynological Zone T from the Maranhão Basin subsurface and the coeval part of the Trombetas Formation from the Amazon Basin to the Lower Silurian-Upper Ordovician is in error. Moreover, I have recovered from the lower Trombetas, well below sections yielding marine phytoplankton, chitinozoans and vertebrates, spore tetrads of Microfossil Assemblage Zone I. Additionally Lange (1972: 38) concluded that strata from the Maranhão Basin which Brito (1967: 480) correlated with the Trombetas Formation of the Amazon Basin on the basis of shared acritatchs should be assigned to the Serra Grande Formation 'probably of Silurian age' and possibly representing lower and part of the middle Llandovery. Colbath (personal communication 1986) regarded the microfossil evidence provided by Bär & Reigel as inconclusive: he wrote '... they haven't illustrated any taxa which require an Ordovician age. They appear to be on safe ground in concluding that the flora is pre-Devonian, but exactly where it belongs in the Silurian is a bit tricky. The diversity of the assemblage suggests an age of approximately middle Llandovery or younger (as does the presence of *Veryhachium carminae*), but that may be an artifact of sampling... Their identification of *Dactylofusa maranhensis* appears reasonable, and does suggest correlation with the Itaim Shale in Brazil.'

Spore tetrads in the Elmina Sandstone confirm a Llandovery age assignment and indicate that the Elmina is older than Brito's Palynological Zone T in the Maranhão Basin and the marine upper Trombetas Formation in the Amazon Basin, but possibly correlative with lower Trombetas that also yields spore tetrads. The large size of the Elmina tetrads (23 (37.8) 50) based on 100 (G1473) measurements suggests mid-Llandovery rather than close to the Ordovician–Silurian systemic boundary. Finally, the sample of Elmina Sandstone collected by Bär & Reigel and later by Gray & Boucot came from a fault sliver in a badly faulted zone (all that was available). There is no assurance that this sample was near the Ordovician–Silurian boundary and there is no palaeontological evidence that requires an age near the boundary.

Manitoulin Island, Ontario, Canada

Spore tetrads come from a palaeokarst sample at, or very close to, the Ordovician-Silurian systemic boundary. The palaeokarst, represented by two surfaces, lies between the Late Ordovician (Ashgill) Kagawong beds and the basal beds of the Early Silurian (Llandovery) Manitoulin Formation on Manitoulin Island, Lake Huron, Ontario, Canada (Kobluk 1984). The boundary lies within the $0.5 \,\mathrm{m}$ which includes the palaeokarst surfaces, but its exact position is controversial. Kobluk, who collected the samples, interprets the palaeokarsts as erosional disconformities which mark subaerially exposed surfaces that resulted from lowered sea-level at the close of the Ordovician.

Midcontinental eastern North America

Spore tetrads have been noted (Gray & Boucot 1972) in latest Ordovician-earliest Silurian beds to either side of the paraconformity that marks the boundary at Ohio Brush Creek, Ohio. Grahn & Bergström (1985: 179) have indicated, from chitinozoans, that this stratigraphical gap represents an interval from the Ashgill *Didymograptus complanatus* Zone to the early Llandovery *Climacograptus cyphus* Zone and 'hence corresponds to about four graptolite zones'—the upper Ashgill (Hirnantian or Gamachian stage) and three graptolite zones of the lowermost Llandovery. Thus the uppermost tetrad-containing Preacherville is no younger than middle Ashgill. Measured spore tetrads represent a single sample from the Preacherville Member of the Drakes Formation (called Elkhorn Formation in Gray & Boucot 1972, Gray *et al.* 1986: fig. 5) and two samples from the lowermost Silurian Belfast Member of the Brassfield Formation (G1385, G1386 from the base of the lower bed; G1384 from 10 inches above G1385 and G1386).

Eastern North America

In New York, north central Pennsylvania, southwestern Virginia, southeastern Tennessee, and northwestern Georgia various rock units to either side and encompassing the Ordovician-Silurian boundary have yielded measurable spore tetrads. These include various Llandovery formations: Whirlpool (Niagara Gorge, New York: Bolton 1957; Martini 1971; Gray & Boucot 1971), Tuscarora (Millerstown, Pennsylvania: Cotter 1982), Hagan Shale Member, Clinch (Hagen, Virginia: Miller & Fuller 1954), Red Mountain (Ringgold, Georgia: Chowns & Howard 1972), and Rockwood (Green Gap and Nickajack Dam, Tennessee: Milici & Wedow 1977). Ashgill Formations include: Red Mountain (Ringgold, Georgia), Shellmound (Nickajack Dam, Tennessee) and Sequatchie (Ringgold, Georgia; Green Gap, Tennessee). There is little independent invertebrate evidence for the age of these shallow-water, nearshore rocks to either side of the Ordovician-Silurian boundary in most of these sections and the amount of section missing at the systemic boundary may be both variable and considerable. The marked change in phytoplankton in boundary rocks reported by Colbath (1983, 1985) is the basis for positioning the boundary within a number of these stratigraphical units, including the Hagan, Nickajack Dam, Green Gap, and Ringgold Sections. Neither the Tuscarora Sandstone nor the Whirlpool (Medina Group) contains diagnostic invertebrate fossils for correlation (Berry & Boucot 1970), although field relations suggest that the lower Tuscarora, in the Millerstown



Section (Cotter 1982) and the Whirlpool, at Niagara Gorge, are early Llandovery (Gray & Boucot 1971).

Brazil

The presence of Silurian rocks in the Paraná Basin, Brazil, has long been at issue. Spore tetrads and phytoplankton (acritarchs and prasinophytes) are both consistent in suggesting a Llandovery age for the Vila Maria Formation, northeast Paraná Basin, southern Brazil, although Gray *et al.* (1985: 524) noted that the spore tetrads are similar in size to Late Ordovician *and* earliest Silurian tetrads whose average sizes are 27 to 29 microns. The Silurian age of the Vila Maria is, however, consistent with the regional geology, including the regional absence of Ordovician rocks.

Sweden

In southern Gotland, well cores at När and Grötlingbo include the entire Silurian below the Wenlock-Ludlow, based on age references provided by *Monograptus* spp., and penetrate the Ordovician-Silurian boundary; in the När core at 380.50 m (Snäll 1977). However, lowermost Silurian graptolites (*M. cometa* Zone?) are first found at 369 m (S. Laufeld, personal communication to A. Le Herisse). According to Le Herisse (personal communication) acritarch assemblages between 385.50 and 380.50 m are Late Ordovician in age, but the interval 380-372 m, characterized by red beds, is largely devoid of organic microfossils, and the 'real Silurian transgression' begins at 372 m where acritarchs and other organic microfossils are abundant. Rare spore tetrads were recovered from När samples (379, 380, 380.50, 382.50, 384 m) by A. Le Herisse, who kindly provided photographs of specimens and small splits of the cores. From three of these samples, 379 m, 380 m and 380.50 m at the Ordovician-Silurian boundary as positioned by Snäll, and 380 m, I recovered sufficient spores to measure.

Czechoslovakia

The Kosov Formation, at Hlasna Trevan near Beroun, on the Berounka River, central Bohemia, has yielded spore tetrads illustrated and described by Vavrdová (1982, 1984). The Kosov Formation corresponds to the latest Ordovician, Upper Ashgill *Glyptograptus bohemicus* Zone (Havlíček & Vaněk 1966; Havlíček & Marek 1973). Vavrdová was kind enough to provide a sample of the Kosov Formation from which abundant spore tetrads were recovered.

South Africa

Spore tetrads are known from the basal Soom Shale Member of the Cedarberg Formation, Table Mountain Group, southwestern Cape Province, South Africa. As discussed by Gray *et al.* (1986), the age of the Cedarberg Formation has been variously interpreted as latest Ordovician (Ashgill) to earliest Silurian (Llandovery) on the basis of limited invertebrate information. Cramer *et al.* (1974) bracketed the Soom Shale as latest Ordovician–earliest Silurian by chitinozoans, but favoured an Ashgill age because of brachiopod data (Cocks & Fortey 1986). Spore size is inconclusive. The measured eight samples also bracket the age of the basal Soom Shale as latest Ordovician–earliest Silurian. However, J. N. Theron's recent discovery of condont assemblages there, considered to be of late Ordovician age by a number of specialists, confirms an Ashgill age for the unit.

Conclusions

These preliminary results, with size frequency measurements, show that the Ordovician-Silurian boundary is bracketed by spore assemblages with spore tetrads having average sizes

Figs 1-6 Scanning electron micrographs of obligate tetrahedral tetrads of spores typical of Microfossil Assemblage Zone I (Gray 1985). Magnification × 1500. All from the Ashgill Preacherville Member, Drakes Formation, Ohio Brush Creek Section, Kentucky, U.S.A. (G1285). Most spore tetrads from Microfossil Assemblage Zone I are smooth-walled (Figs 1, 5), and some have an outer envelope that may be shed. The outer envelope is most commonly reticulate (Figs 2, 4, 6). Fig. 3 shows a spore tetrad with a smooth-walled envelope or possibly a degraded reticulate envelope.

less than 30 microns. The average size of spore tetrads to either side of the boundary, as positioned by palaeontological or micropalaeontological data, or by a stratigraphical gap and change in lithology, is about 26–29 microns, although there are both smaller (Sequatchie Formation) and larger spore tetrads (Manitoulin palaeokarst) known from rock units close to, or at, the systemic boundary. Slight differences in spore tetrad size on opposite sides of the boundary are inadequate, without other evidence, to distinguish latest Ordovician from earliest Silurian age rocks, although the Ordovician–Silurian boundary is easily bracketed by spore assemblage measurements.

I have no explanation for the relatively small size of the spore tetrads from the Sequatchie Formation. The measured samples may be lower in the Sequatchie, i.e. older, than now recognized in terms of their stratigraphical position relative to the Ordovician-Silurian boundary. possibly related to the presence of a significant disconformity. I have no independently dated assemblages from within the Ashgill for comparative purposes. With small microfossils, there is always the possibility of independent size-sorting, since these fossils behave as clastic sedimentary particles with hydraulic equivalents in the fine or very-fine silt size fraction (Stanley 1969: Muller 1959; Brush & Brush 1972). Water turbulence can keep large quantities of pollen or spores in suspension for extended periods, and it may be that the smaller spore tetrads of the Sequatchie were winnowed from the spore assemblage through progressive sorting and deposited with finer mineral particles, possibly in a more off-shore environment than represented by the depositional environments of many of the other units, or in a pattern related to marine currents or some other hydrodynamic factors. This phenomenon may also account for some of the inconsistencies found in a few of the other measurements. The large size of the Manitoulin tetrads is not consistent with the other results and a more serious threat to the utility of spore-size measurements for discriminating the Ordovician-Silurian boundary, since the stratigraphical position of the sample seems well fixed. The comparatively large size of these spores, for which only relatively few measurements were available, may reflect the fact that this sample was not originally extracted for spores, but for arthropod cuticle remains, so that smaller tetrads may have been lost in the sieving process. This material is being re-extracted specifically to recover spores and measurements repeated on a larger number of spore tetrads.

Acknowledgements

I would like to thank A. J. Boucot for discussion of stratigraphical data, A. Le Herisse and M. Vavrdová for supplying sediment samples, and G. K. Colbath for information on the acritarchs from the Elmima Formation.

Appendix

Size measurements of Ashgill and Early Llandovery spore tetrads

Lower Llandovery	Ν	Min.	Aver.	Max.
Robert Moses Power Plant Section, Niagara Falls, New York				
Whirlpool Sandstone (G1189)	250	13	26.5	44
Millerstown Section, Pennsylvania				
Tuscarora Formation (G1408)	100	18	27.0	41
Tuscarora Formation (G1407)	100	17	27.3	47
Tuscarora Formation (G1406)	100	17	28.0	49
Tuscarora Formation (G1374)	150	16	27.5	45
Nickajack Dam Section, Tennessee				
Rockwood Formation (ND70)	41	22	33.6	51
Rockwood Formation (ND54)	107	15	29.9	53
Ringgold Section, Georgia				
Red Mountain Formation (RN570)	200	15	26.6	39
Red Mountain Formation (RN470)	86	17	29.4	48
Red Mountain Formation (RN420)	45	17	27.8	39
Red Mountain Formation (RN370)	148	13	25.6	38
Red Mountain Formation (RN320)	98	13	26.9	45

Hagan Section, Virginia	N	Min.	Aver.	Max.
Hagan Shale Member, Clinch Formation (HGII70)	200	13	29.2	49
Hagan Shale Member (HGII50)	135	19	32.2	54
Hagan Shale Member (HG1130)	87	18	29.7	49
Hagan Shale Member (HG1110)	215	13	27.5	47
Ohio Brush Creek Selection, Ohio				
Belfast Member, Brassfield Formation (G1384)	100	17	26.9	39
Belfast Formation (G1385)	100	18	27.3	45
Belfast Formation (G1386)	150	17	27.0	40
Narborrningen 1, southern Gotland, Sweden				
Unnamed formation, 379.00 m (G1553)	25	19	28.8	41
Unnamed formation, 380.00 m (G1549)	69	20	28.6	52
Unnamed formation, 380-50 m (G1548)	34	19	29.8	40
Fazenda Tres Barras Section, Brazil				
Vila Maria Formation (G1391)	150	18	29.1	42
Ashaill				
Swartleikloff Section, South Africa				
Soom Shale Member Cedarberg Formation (G1363)	100	15	27.5	40
Soom Shale Member (G1364)	100	17	27.5	27
Soom Shale Member (G1365)	100	20	28.3	37 A1
Soom Shale Member (G1366)	100	17	20.4	20
Soom Shale Member (G1367)	100	22	27.5	39 40
Soom Shale Member (G1368)	100	17	28.7	40
Soom Shale Member (G1369)	100	20	20.6	40
Soom Shale Member (G1370)	100	17	29.0	45
Combined average	800	15	29.2	45
Hlasna Trehan Section Bohemia	108	15	28.0	45
Kosov Formation (G1430)	100	10	20.0	41/
Paleokarst at Ordovician-Silurian systemic boundary				
Manitoulin Island, Ontario (G1272)	45	22	33.0	46
Ohio Brush Creek Section Kentucky	10	~~	550	40
Preacherville Member Drakes				
Formation (G1285)	252	17	27.5	53
Green Gap Section. Tennessee	202	1,	21.5	55
Sequatchie Formation (GG19)	58	12	22.0	32
Nickajack Dam Section Tennessee	00		22.0	
Shellmound Formation (ND33)	150	18	26.5	50
Shellmound Formation (ND20-5)	141	16	20 3	43
Ringgold Section, Georgia	• • •	10	211	45
Red Mountain Formation (RN210)	59	16	25.6	41
Red Mountain Formation (RN201)	89	14	23.9	46
Sequencing Formation ($\mathbb{R}N195 = G1245$)	200	11	23.2	40
Sequatchie Formation (G1245)	100	11	24.0	46
Sequatchie Formation (G1246)	100	14	23.7	50
Sequatchie Formation (RN139)	66	14	24.4	35
				~~

Notes: The samples are in stratigraphical order within each section, with the youngest at the top. G numbers are Gray extractions; others are Colbath extractions. G1385, G1386 were measured from samples collected along the strike.

References

- Bär, P. & Riegel, W. 1980. Mikrofloren des höchsten Ordovizium bis tiefen Silurs aus der Unteren Sekondi-Serie von Ghana (Westafrika) und ihre Beziehung zu den Itaim-Schichten des Maranhão-Beckens in NE-Brasilien. N. Jb. Geol. Paläont. Abh., Stuttgart, 160: 42–60.
- Berry, W. B. N. & Boucot, A. J. (eds) 1970. Correlation of the North American Silurian Rocks. Spec. Pap. geol. Soc. Am., Boulder, Col., 102: 1–289.
- Bolton, T. E. 1957. Silurian stratigraphy and palaeontology of the Niagara escarpment in Ontario. Mem. geol. Surv. Brch Canada, Ottawa, 289: 1-145.

- Brito, I. M. 1967. Silurian and Devonian acritarchs from Maranhão Basin, Brazil. *Micropaleontology*, New York, 13: 473–482.
- Brush, G. S. & Brush, L. M. 1972. Transport of pollen in a sediment laden channel: a laboratory study. Am. J. Sci., New Haven, 272: 359–381.
- Chowns, T. M. & Howard, J. H. 1972. Section of Ordovician and Silurian strata exposed in road cuts on I-75 at Ringgold Gap, Georgia. In T. M. Chowns (ed.), Sedimentary environments in the Paleozoic rocks of northwest Georgia. Guidebk Dep. Mines Min. Geol., Ga, Atlanta, 11: 97-100.
- Cocks, L. R. M. & Fortey, R. A. 1986. New evidence on the South African Lower Palaeozoic: age and fossils reviewed. *Geol. Mag.*, Cambridge, 123: 437-444.
- Colbath, G. K. (1983). Paleoecology of palynomorphs from the Upper Ordovician-Lower Silurian of the Southern Appalachians, U.S.A. Ph.D. thesis, Univ. Oregon, Eugene. 314 pp. (unpubl.)
- 1986. Abrupt terminal Ordovician extinction in phytoplankton associations, southern Appalachians. Geology, Boulder, Colo., 14 (11): 943–946.
- Cotter, E. 1982. Tuscarora Formation of Pennsylvania (Guidebook 1982 Field Trip). 105 pp. Soc. Econ. Paleont. Min., Eastern Sect.
- Cramer, F. H., Rust, I. C. & Diez de Cramer, M. deC. R. 1974. Upper Ordovician chitinozoans from the Cedarberg Formation of South Africa. Preliminary Note. *Geol. Rdsch.*, Stuttgart, 63: 340-345.
- Grahn, Y. & Bergström, S. M. 1985. Chitinozoans from the Ordovician-Silurian boundary beds in the Eastern Cincinnati Region in Ohio and Kentucky. Ohio Acad. Sci. 85 (4): 175-183.
- Gray, J. 1985. The microfossil record of early land plants: advances in understanding of early terrestrialization, 1970-1984. Phil. Trans. R. Soc., London, (B) 309: 167-195.
- & Boucot, A. J. 1971. Early Silurian spore tetrads from New York: earliest New World evidence for vascular plants? *Science*, N.Y. 173: 918–921.
- 1972. Palynological evidence bearing on the Ordovician–Silurian paraconformity in Ohio. Bull. geol. Soc. Am., New York, 83: 1299–1314.
- 1975. Color changes in pollen and spores: A review. Bull. geol. Soc. Am., Boulder, Col., 86: 1019–1033.
- —, Colbath, G. K., de Faria, A., Boucot, A. J. & Rohr, D. M. 1985. Silurian-age fossils from the Paleozoic Paraná Basin, southern Brazil. *Geology, Boulder, Colo.*, 13: 521–525.
- —, Theron, J. N. & Boucot, A. J. 1986. Age of the Cedarberg Formation, South Africa and early land plant evolution. *Geol. Mag.*, Cambridge, 123: 445–454.
- Havlíček, V. & Marek, L. 1973. Bohemian Ordovician and its international correlation. Cas. Miner. Geol., Prague, 18: 225–232.
- & Vaněk, J. 1966. The biostratigraphy of the Ordovician Bohemian. Sb. geol. Věd., Prague, (Paleont.) 8: 7–69.
- Kobluk, D. R. 1984. Coastal paleokarst near the Ordovician-Silurian boundary, Manitoulin Island, Ontario. Bull. Can. Petrol. Geol., Calgary, 32 (4): 398-407.
- Lange, F. W. 1972. Silurian of Brazil. In W. B. N. Berry & A. J. Boucot (eds), Correlation of the South American Silurian Rocks. Spec. Pap. geol. Soc. Am., Boulder, Col., 133: 33-39.
- Martini, I. P. 1971. Regional analysis of sedimentology of Medina Formation (Silurian), Ontario and New York. Bull. Am. Ass. Petrol. Geol., Tulsa, Ok., 55: 1249–1261.
- Milici, R. C. & Wedow, H. 1977. Upper Ordovician and Silurian stratigraphy in Sequatchie Valley and parts of the adjacent Valley and Ridge, Tennessee. *Prof. Pap. U.S. geol. Surv.*, Washington, 996: 1–38.
- Miller, R. L. & Fuller, J. O. 1954. Geology and oil resources of the Rose Hill district-the Fenster area of the Cumberland overthrust block-Lee County, Virginia. *Bull. Va geol. Surv.*, Charlottesville, 71: 1–383, 4 maps.
- Muller, J. 1959. Palynology of recent Orinoco Delta and shelf sediments. *Micropaleontology*, New York, 5: 1–32.
- Quadros, L. P. de 1985. Natureza do contato entre as formações Trombetas e Maecuru (Bacia do Amazonas). In: Coletanea de Trabalhos Paleontologicos, Paleontologia e Estratigrafia 2 (Trabalhos Apresentados No. VIII Congresso Brasileiro de Paleontologia, 1983): 435-441.
- Snäll, S. 1977. Silurian and Ordovician bentonites of Gotland (Sweden). Stockh. Contr. Geol., 31 (1): 1-80.
- Stanley, E. A. 1969. Marine palynology. Oceanography mar. Biol., London, 7: 277-292.
- Vavrdová, M. 1982. Recycled acritarchs in the upper Ordovician of Bohemia. Cas. Miner. Geol., Prague, 27: 337-345.
 - 1984. Some plant microfossils of possible terrestrial origin from the Ordovician of Central Bohemia. *Věst. ustřed. Úst geol.*, Prague, **59:** 165–170.